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Specific niche requirements underpin multidecadal range edge stability, but may introduce barriers for climate change adaptation

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Abstract

Aim: To investigate some of the environmental variables underpinning the past and present distribution of an ecosystem engineer near its poleward range edge.

Location: >500 locations spanning >7,400 km around Ireland.

Methods: We collated past and present distribution records on a known climate change indicator, the reef-forming worm *Sabellaria alveolata* (Linnaeus, 1767) in a biogeographic boundary region over 182 years (1836–2018). This included repeat sampling of 60 locations in the cooler 1950s and again in the warmer 2000s and 2010s. Using species distribution modelling, we identified some of the environmental drivers that likely underpin *S. alveolata* distribution towards the leading edge of its biogeographical range in Ireland.

Results: Through plotting 981 records of presence and absence, we revealed a discontinuous distribution with discretely bounded sub-populations, and edges that coincide with the locations of tidal fronts. Repeat surveys of 60 locations across three time periods showed evidence of population increases, declines, local extirpation and recolonization events within the range, but no evidence of extensions beyond the previously identified distribution limits, despite decades of warming. At a regional scale, populations were relatively stable through time, but local populations in the cold Irish Sea appear highly dynamic and vulnerable to local extirpation risk. Contemporary distribution data (2013–2018) computed with modelled environmental data identified specific niche requirements which can explain the many distribution gaps, namely wave height, tidal amplitude, stratification index, then substrate type.

Main conclusions: In the face of climate warming, such specific niche requirements can create environmental barriers that may prevent species from extending beyond their leading edges. These boundaries may limit a species' capacity to redistribute in response to global environmental change.

KEYWORDS

biogenic habitat, biogeography, cold event, Irish Sea, macroecology, tidal front

1 | INTRODUCTION

Climate change poses a major threat to biodiversity through driving the global redistribution of species (Parmesan et al., 1999). At leading edges, warming temperatures can drive range extensions of organisms (Burrows et al., 2011), although cool summer or winter temperatures and extreme weather events can affect survival or reproductive success (Firth et al., 2011; Hutchins, 1947), which can limit range extension. If the leading edge adjoins a stretch of unfavourable habitat or a physical barrier to movement, individuals of a species may have 'nowhere to go' (Loarie et al., 2009). If the trailing edge 'catches up' with the leading edge, a species may be susceptible to local extirpation or even be at risk of global extinction (Marzloff et al., 2018), unless individuals can adapt to changing environmental conditions.

In the marine environment, mesoscale nearshore circulation patterns are modified by shoreline configuration, bathymetry and

tides creating eddies or fronts, sharp discontinuities of physical and chemical variables characterized by different temperatures and/or salinities and hence density regimes (e.g. Pineda, 1994; Simpson & Hunter, 1974). Seasonal tidal mixing fronts, such as those found in northwest France (Le Boyer et al., 2009) or in the Irish Sea (Simpson et al., 2009), form within a few days and persist for only a few months before their dissipation. Other fronts, such as the southern Antarctic Circumpolar Current front (Orsi et al., 1995) can persist for longer and are quasi-permanent features in the ocean. Tidal mixing fronts separate vertically well-mixed and stratified water columns. They are often enriched in nutrients on the stratified side as the surface layer is usually shallower than the photic zone, leading to enhanced primary production (Sharples, 2008). When they occur, the spatially stratified environmental conditions they represent can act as barriers to dispersal for a range of taxa including fish and invertebrates (Galarza et al., 2009) and can adversely affect individual survivorship, thus making fronts potentially strong

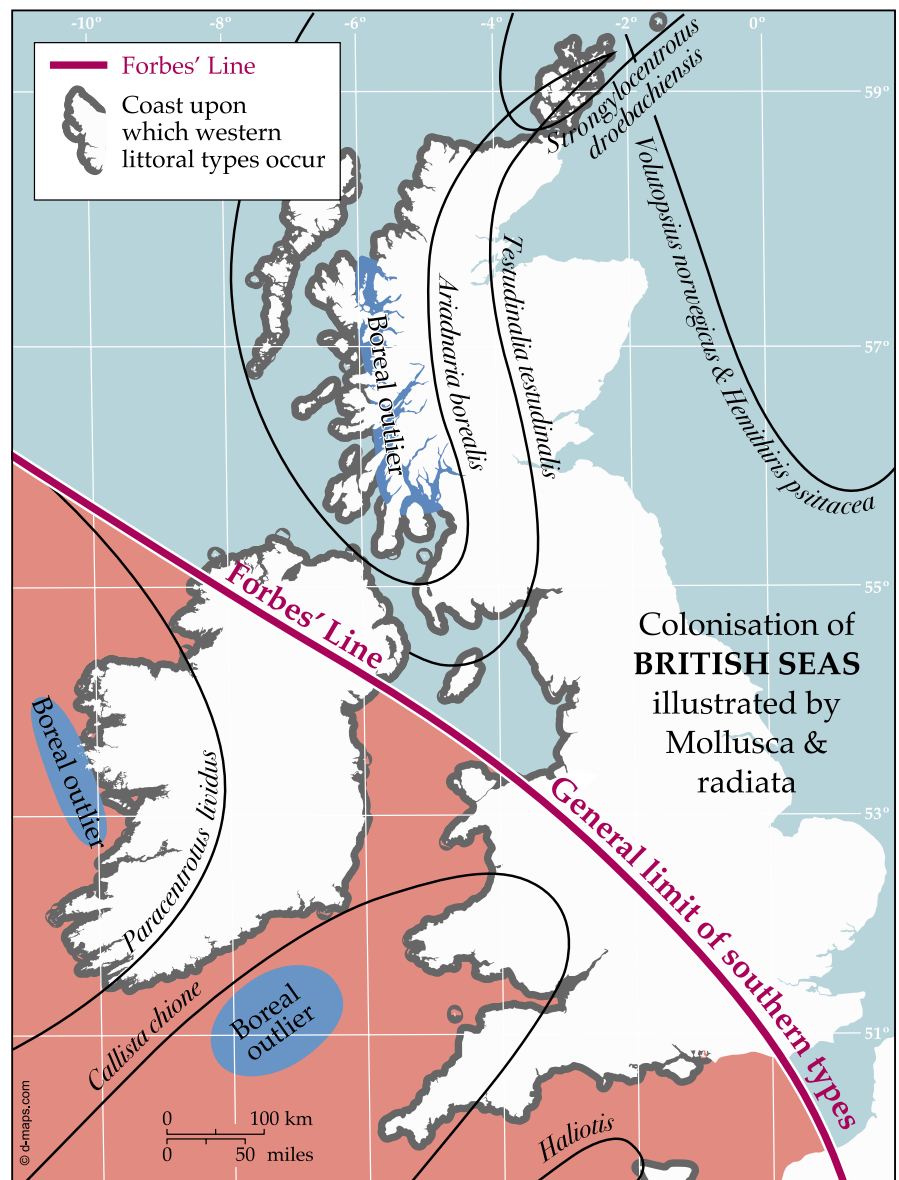
structural determinants of species distributions signified by clusters of range edges around them (e.g. Gaylord & Gaines, 2000; Sagarin et al., 1999).

Given that dispersal is a key process shaping the distribution of marine species by mediating connectivity and recruitment within and among patches (James et al., 2019), the presence and duration of fronts could affect the dispersal and population dynamics of a species, thereby affecting long-term trends in abundance and distribution (Ayata et al., 2010; Pringle et al. 2017). For instance, Banks et al. (2007) showed how a front created a persistent cold-water barrier that has prevented further advancement and colonization of the south coast of Tasmania by the invasive urchin *Centrostephanus rogersii*. Consequently, range extension (or lack of) and species responses around fronts and other barriers to movement (e.g. habitat continuity, Fenberg & Rivadeneira, 2019) may well be idiosyncratic to more general predictions of range extensions under climate change scenarios. Hence, there is a need for more work in these areas if we

are to better understand patterns and trends in biogeography and inform conservation.

A number of fronts are found around the islands of Ireland and Britain which straddle a biogeographic boundary between cold 'Boreal' and warmer 'Lusitanian' waters. Forbes (1858) produced the first map of the broad distributional limits of marine species of Britain and Ireland with a line depicting the 'general limit of southern types' (herein "Forbes' Line," Figure 1). In response to recent warming, many species have exhibited range extensions beyond previously known limits that coincided with this line in Britain; both northwards through the Irish Sea and eastwards along the English Channel (Mieszkowska et al., 2005, 2014; Southward et al., 1995). In contrast to the surrounding warmer waters of the Atlantic Ocean and Celtic Sea, the Irish Sea is dominated by cooler, mixed water in summer (Simpson & Hunter, 1974, Figure 2a). During the summer, several tidal fronts appear, two of which roughly coincide with Forbes' Line. To the north and south, the Islay and Celtic Sea

FIGURE 1 Biogeographical characteristics of the coasts of Ireland and Great Britain based on the range limits of some species; redrawn from Forbes (1858). The original map identified the "general limit of southern types" which is denoted here as "Forbes' Line." The line intersects the Irish coast near Bloody Foreland, Co. Donegal on the west coast and Dundrum Bay, Co. Down on the east coast; it intersects the British coast at the Isle of Anglesey (missing from the original map) on the west coast and near Beachy Head on the south coast. It also intersects the French coast just west of Dieppe, Normandy. Species listed in Forbes' original map: the limpet *Testudinalia testudinalis* (formerly *Acmaea testudinalis*); the bivalve *Callista chione* (formerly *Cytherea chione*); the snails *Volutopsis norvegicus* (formerly *Fusus norvegicus*), *Hemithiris psittacea* (formerly *Rhynchonella psittacea*), *Ariadnaria borealis* (formerly *Trichotropis borealis*), the urchins *Paracentrotus lividus* (formerly *Echinus lividus*), *Strongylocentrotus droebachiensis* (formerly *Echinus neglectus*) and the abalone *Haliotis* is *Haliotis tuberculata*. Map created by Tim Absalom, University of Plymouth GeoMapping Unit



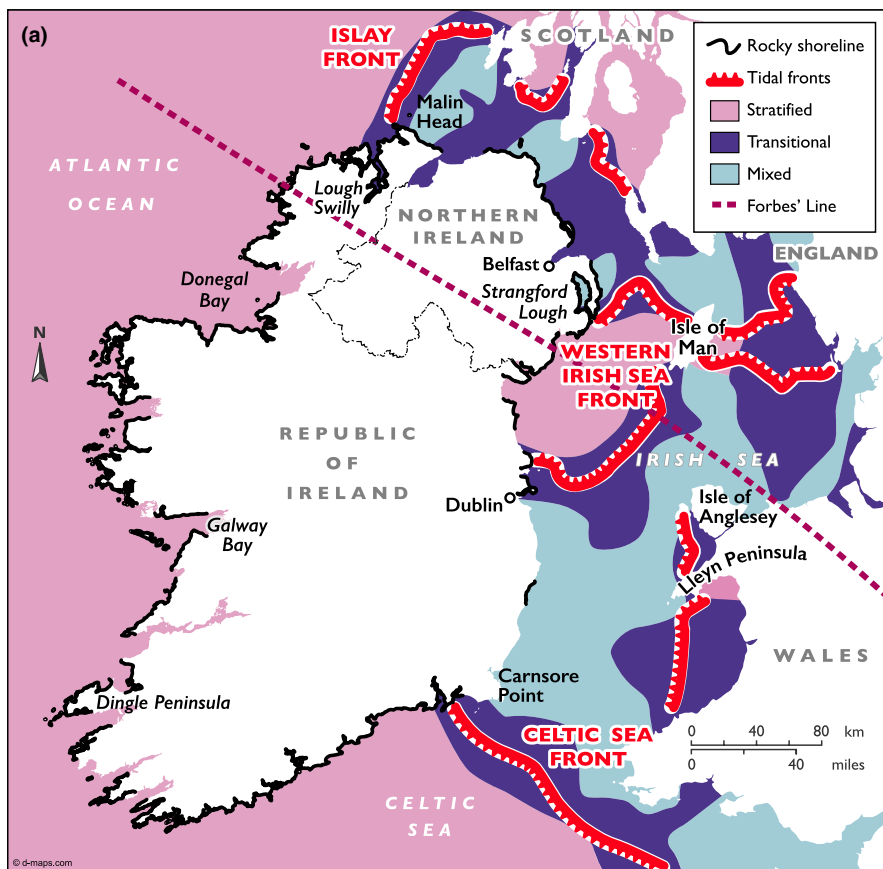
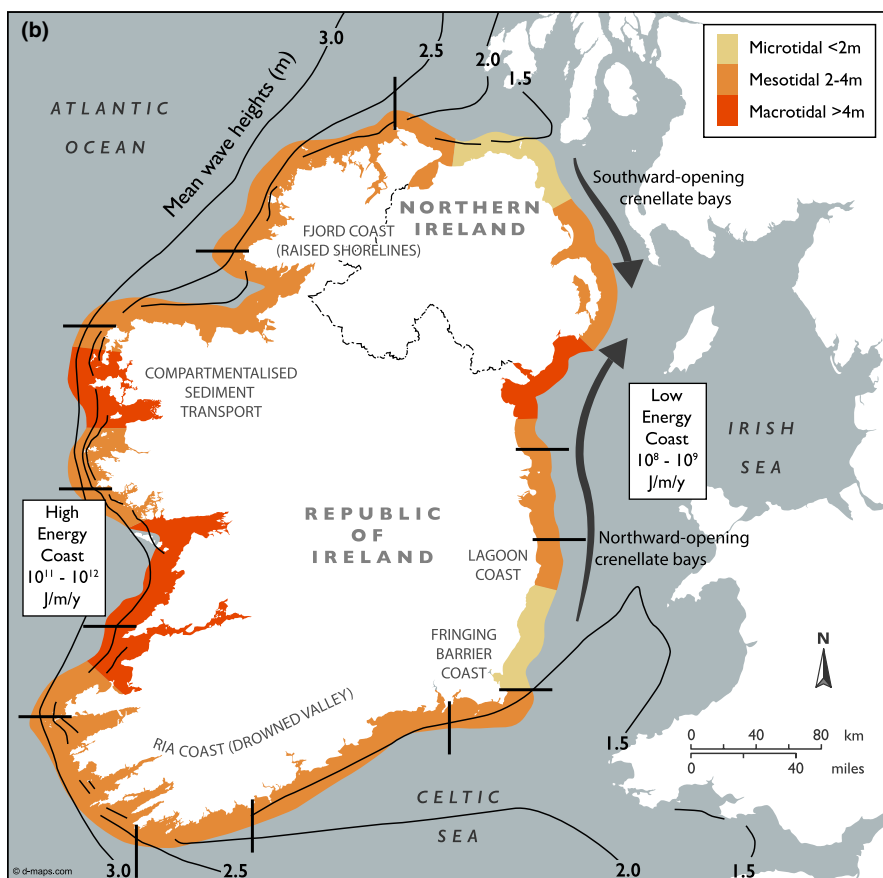


FIGURE 2 Habitat maps showing physical and hydrographic features in relation to Forbes' Line. (a) The distribution of rocky coastline, tidal fronts and summer water types (stratified, transitional, mixed) around Ireland (composite map redrawn from Devoy, 2008; Pingree & Griffiths, 1978). For more detail on spatio-temporal variation in sea surface temperature see Figure S1. (b) Coastal configuration, spatial changes in wave climate and variation in spring tidal ranges around Ireland (map redrawn from Devoy, 2008 with wave heights from Bricheno & Wolf, 2018). Maps created by Tim Absalom, University of Plymouth GeoMapping Unit



Fronts separate the cold water of the Irish Sea from the warmer Atlantic Ocean and Celtic Sea, respectively (Figure S1). Within the Irish Sea, a patch of warm water develops in the summer that is bounded by the Western Irish Sea Front and the Western Irish Sea gyre. This creates a mosaic of patches of warmer and cooler waters around the island.

Crisp (1989) was one of the first to describe the influence of tidal fronts on the distribution of intertidal taxa. He described a positive association between the reef-forming worm *Sabellaria alveolata* (Linnaeus, 1767), the topshell *Phorcus lineatus* (da Costa, 1778) and chthamaliid barnacles (all warm-affinity taxa) with the patch of warm summer-stratified water bounded by the Western Irish Sea Front (Figure 2a). Since Crisp (1989), surprisingly little research has been done, on either investigating patterns of distribution of intertidal taxa in relation to tidal fronts, or indeed the mechanisms underpinning these patterns (but see Ayata et al., 2010). The presence of so many tidal fronts combined with a complex coastline (Figure 2b) and a mosaic of mixed and stratified waters in a biogeographic boundary region presents an ideal study system for testing hypotheses about proximate environmental factors determining the range edges of climate change indicators at their poleward edge of distribution.

The honeycomb worm, *S. alveolata* is protected under the EU Habitats Directive because it is considered an ecosystem engineer that creates a range of biogenic structures (sheets, veneers, hummocks to the largest reefs in Europe, Curd, et al., 2019), which provide habitat for a multitude of other species throughout its geographic range (Cole and Chapman, 2007; Plicanti et al., 2017; Jones et al., 2018). Its planktotrophic larvae settle and metamorphose preferentially on the cemented sand tubes of conspecific adults (Wilson, 1968), typically in areas where rocky reefs abut sandy beaches that can supply coarse sand for tube-building (Firth et al., 2015). It is often described to be distributed from North Africa to southwest Scotland (Dubois et al., 2002), but it is also present in Ireland (Culloty et al., 2010). Despite very little being known about its distribution in Ireland (only 40 records in Oceanographic Biodiversity Information System (OBIS) database, representing 1.6% of total records), Crisp (1989) identified a leading edge on the east coast in the northern Irish Sea. It is possible that another leading edge exists on the northwest coast where it was also known to occur in the past (Duerden, 1895). In Britain, where there is a strong heritage of sustained observations (Hawkins et al., 2013; 2,357 records in OBIS database, representing 93.6% of records), it is considered a climate change indicator that is expected to benefit from climate change (Mieszkowska et al., 2013) due to exhibiting population increases in response to warming temperatures (Mieszkowska et al., 2005) and decreases in response to extreme cold events (Crisp, 1964; Firth et al., 2015). Bush (2015) identified the leading edge in Britain to be in the northern Irish Sea at Auchenmalg, southwest Scotland.

Here, we investigated some of the environmental variables underpinning the distribution of *S. alveolata* around Ireland. We combined historical data from a range of sources with contemporary data from broad-scale field surveys to describe past and present distributions to build up a detailed picture of the fine-scale distribution.

Building on existing comprehensive unpublished datasets from the 1950s and 2000s, we revisited 60 target locations, alongside many more (283) in the 2010s to quantify spatio-temporal changes in distribution and abundance during a period of rapid warming. Then, using a habitat suitability modelling approach, we assessed some of the environmental drivers which we considered to be important in underpinning the distribution of *S. alveolata*. The outputs provide insights into some of the environmental variables underpinning the biogeography of this key ecosystem engineer and will help to inform conservation and management plans for a species that may be susceptible to climate change and other anthropogenic stressors.

2 | METHODS

2.1 | Mapping of past and present distributions

2.1.1 | Compilation of historical data

Data on the distribution and abundance of *S. alveolata* around Ireland were collated from a range of sources, including targeted surveys, field notebooks, grey literature, museum specimens, personal communications, and publicly available databases (e.g. National Biodiversity Data Centre; Global Biodiversity Information Facility; UK National Biodiversity Network, see Appendix S1 for full list of data sources). Furthermore, all 14 synonyms for *Sabellaria alveolata* (as identified in the World Register of Marine Species) were used in searches for historical records in published literature. These data were reported in a range of different ways; many reported abundance scores based on the semi-quantitative SACFOR scale (S = Superabundant, A = Abundant, C = Common, F = Frequent, O = Occasional, R = Rare, and Not Seen, see Table S1 for descriptions), some estimated abundances per unit area, whilst others simply noted presences. Where a SACFOR classification was not specified, we assigned 'present'. All records that were not collected by the authors were carefully scrutinized and any dubious records were omitted.

Comprehensive island-wide surveys were conducted at the same 60 locations in the 1950s (Southward & Crisp, 1954), 2000s (Simkanin et al., 2005) and in the 2010s. The 2010s surveys were done by authors of this paper, who also revisited an additional 75 locations sampled in either the 1950s or 2000s, along with 208 new locations to chart the broad-scale distribution of *S. alveolata* on different shore types. For these surveys, *S. alveolata* abundance was estimated following a 30-min search at each location (typically by two people, covering up to 1000 m² depending on the topography) using the modified semi-quantitative SACFOR abundance scale (Table S1). Following the methodology of Firth et al. (2015), 'Abundant' and 'Superabundant' were combined as 'Abundant' to ensure comparability with Crisp and Southward, as 'Superabundant' was adopted in the 1970s. Changes in abundance were considered in two ways—a conservative two-category change (e.g. Frequent to Abundant) and a less conservative one-category change.

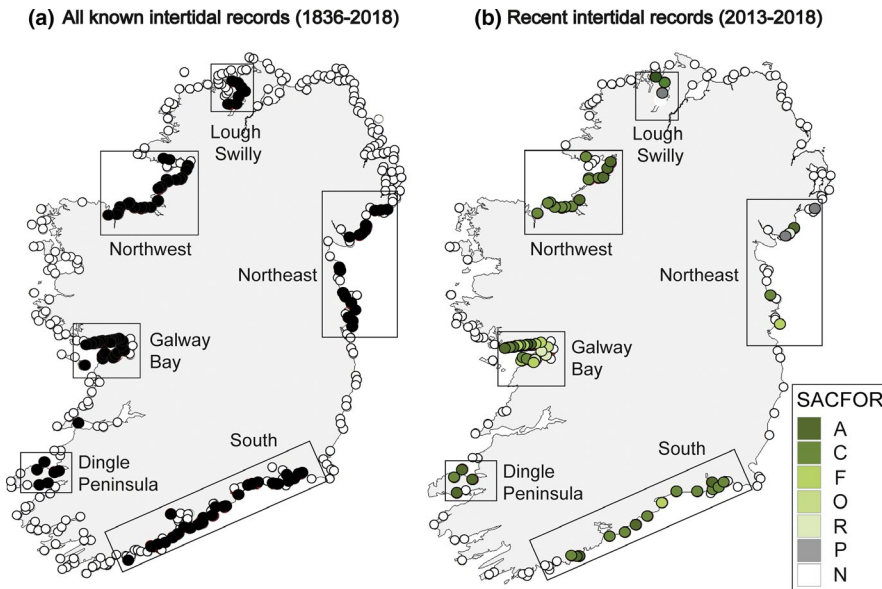


FIGURE 3 Map illustrating the locations around Ireland where *Sabellaria alveolata* was ever recorded as present. Full circles = known presences; empty circles = known absences; Boxes illustrate discretely bounded regional sub-populations: the northeast; the south; Dingle Peninsula; Galway Bay; northwest; Lough Swilly. (a) Intertidal distribution including 954 records spanning 1836 to 2018. (b) The present distribution and SACFOR estimates of *S. alveolata* in intertidal habitats collected during the 6-year period from 2013–2018. Only data collected by the authors are presented for 2013–2018. A = Abundant; C = Common; F = Frequent; O = Occasional; R = Rare

2.2 | Distribution modelling

Based on the 2013–2018 surveys and a collation of metrics related to coastal features and recent ocean and atmospheric variables, we characterized some of the environmental factors that we considered to be important in determining *S. alveolata* occurrence around Ireland. The 348 SACFOR records available since 2013 were converted to 176 presence/absence records gridded within 5×5 km cells to thin out adjacent observations and match the spatial resolution of most environmental variables. A total of 12 environmental variables, characterizing coastal ocean and atmospheric features of potential relevance to *S. alveolata* ecology, were selected as follows: out of an original set of 64 variables corresponding to coastal features and climatological summary statistics derived from available time series (e.g. mean, maximum, minimum and relevant quantiles; see Appendix S2) for dynamic variables, we proceeded to a stepwise variable selection so as to maintain the lowest multicollinearity among the variables, using an individual Variance Inflation Factor (VIF) threshold below 10 (Craney & Surlles, 2002). The final list of predictors included significant wave height (Bricheno & Wolf, 2018); tidal amplitude (TPX09, Egbert & Erofeeva, 2002; Egbert et al., 2010; data available from <https://www.tpxo.net/global>); salinity, mean and minimum sea surface temperature (SST, Amo et al., 2019); front persistence, mean and fifth percentile of distance to closest front, and front side—whether cell is on cold (−1) or warm (+1) side of closest front (Miller et al., 2015); wind speed (Météo France ARPEGE model; Déqué et al., 1994); stratification index (Crisp, 1989: $SI = \log_{10}(H/u^3)$, where H corresponds to water depth estimated from EMODnet Bathymetry and u to vertically averaged current velocity estimated from the *IBI_ANALYSIS_FORECAST_PHYS_005_001* model available via CMEMS), and substrate type (EMODnet Geology). Details about environmental variable resolutions and sources are provided in Appendix S2.

Intertidal habitat substrata were categorized as rock and boulders, coarse substrate, sand, muddy sand, sandy mud, mud, and mixed sediments. Due to lack of habitat information, five data points were excluded from analysis from the Connemara coastline (central-west region). To assess sensitivity to alternative distribution modelling techniques, in the first instance we fitted generalized linear models (GLM), generalized additive models (GAM), multivariate adaptive regression splines (MARS), random forests (RF) and boosted regression trees (BRT), as well as support vector machines (SVM) models to presence/absence data using the *sdm* R package (Naimi & Araújo, 2016). Using default model settings, all methods yielded similar results both in terms of variable influences on predicted probability of presence and cross-validation accuracy levels (i.e. area under the curve (AUC) varied from 0.81–0.91 for GAM and SVM, respectively). Following guidance in Elith et al., (2008), BRT models underwent further tuning leading to being adopted after achieving the highest AUC (~0.92 on 10-fold random cross-validation versus ~0.88 on 10-fold cross-validation with spatial blocks) of all models. Briefly, this AUC score was achieved by fitting a Bernoulli distribution, implemented in the *gbm.step* function of the *dismo* package v. 1.1-4 (Hijmans et al., 2017) in R v. 3 (R Core Team, 2020) with a learning rate of 0.001, tree complexity of 5, and a bag fraction of 70% (meaning that at each iteration of the model, 70% of the data are drawn at random, without replacement, from the training set). Cross-validation accuracy levels were based on 10-fold cross-validation and spatial blocks assuming a ~67 km autocorrelation range as estimated on the 11 quantitative environmental layers (excluding substrate type) using the *blockCV* R package (Valavi et al., 2019). Folds were stratified by prevalence so that each fold roughly contained the same proportion of presences and absences. Relative importance of each explanatory variable (determined by the reduction in root mean square error (RMSE) following introduction of a variable) and partial dependencies were produced using the *ggbrt* package (Jouffray et al., 2019).

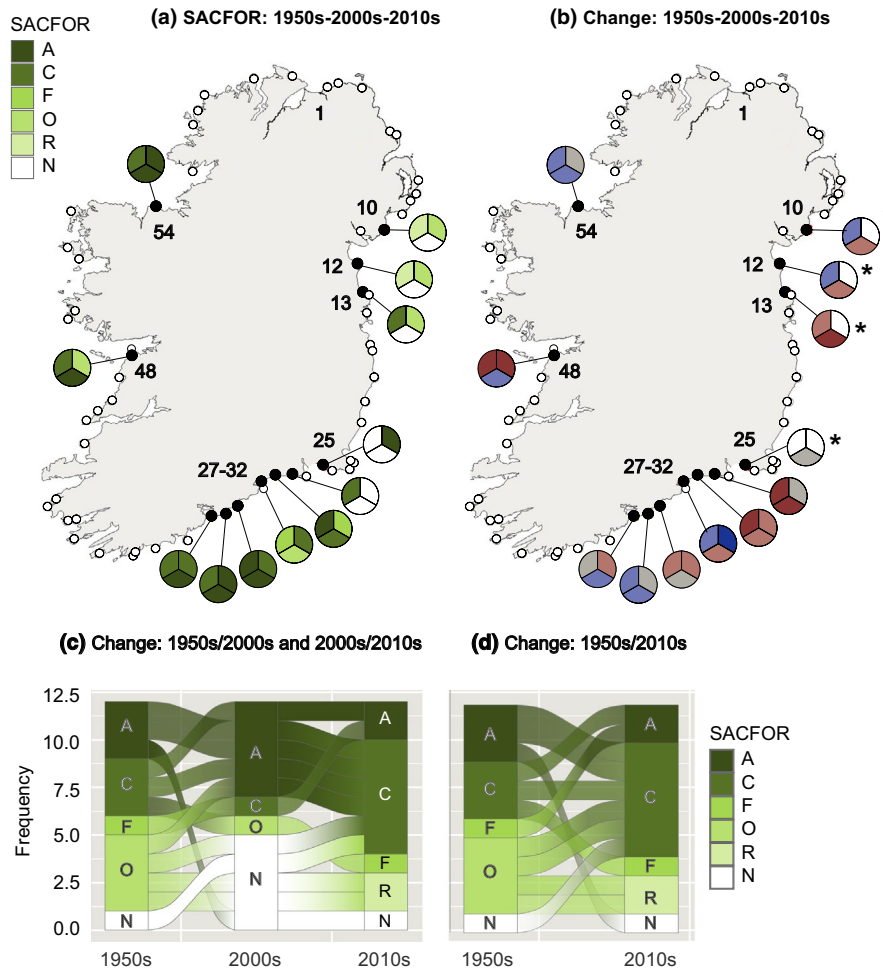


FIGURE 4 Spatio-temporal comparison of distribution and abundance of *Sabellaria alveolata* across 60 survey locations that were common to the Crisp/Southward surveys in the 1950s (1952 and 1958), the surveys in the 2000s (2003/2004) and the recent surveys by authors in the 2010s (2013/2014). (a) Pie charts are only shown for locations in which *S. alveolata* was present in at least one time period. All other locations where *S. alveolata* was absent in all three time periods are shown as white dots. Pie charts show SACFOR abundance score for each of the three time periods for each location. Top right segment = 1950s; bottom segment = 2000s; top left segment = 2010s. The number 1 is inserted for illustrative purposes to indicate where location numbering begins. (b) Pie charts showing relative change between sampling periods for each location. Top right segment = 1950s/2000s; bottom segment = 2000s/2010s; top left segment = 1950s/2010s; light and dark pink denote 1- and >2-step increases, respectively; light and dark blue denote 1- and > 2-step decreases, respectively; grey denotes no change; white * = denotes potential extirpations. (Note: The 2010 data point for location 12 was not collected by the authors of this paper and was assigned a conservative Rare on the SACFOR scale). (c, d) Sankey charts showing the frequency of SACFOR estimates in each sampling period and relative changes between periods. See Table S2 for list of survey locations. A = Abundant; C = Common; F = Frequent; O = Occasional; R = Rare; N = Not seen

3 | RESULTS

3.1 | Mapping of past and present distributions

A total of 981 records spanning 182 years (1836–2018) and the whole coastline of Ireland were collated during this study, comprising 319 presences (33%) and 662 absences (not seen) (67%) (data available in Curd, Cordier, et al., 2020). 776 (79%) records were collected by either the authors of this paper or by Crisp and Southward. The remaining 205 (21%) were from a combination of online databases, unpublished theses, reports, published papers and museum specimens. The vast majority of the records (954; 97%) were from intertidal surveys (Figure 3a). Given the paucity of subtidal records, we focus on the intertidal dataset.

Sampling effort varied spatially and temporally (Figure S2). *Sabellaria alveolata* exhibited a discontinuous distribution with six discretely bounded regional sub-populations (Figure 3a). It was found at a large number of locations along the south coast (Cullenstown, Co. Wexford to Galley Head, Co. Cork), in Galway Bay, and in the northwest (Killala Bay, Co. Mayo to Fintra Beach, Co. Donegal). It was also found in smaller pockets on the Dingle Peninsula in the southwest, in Lough Swilly on the north coast, and along the northeast coast (Coney Island, Co. Down to Howth, Co. Dublin, where it was typically less abundant (i.e. exhibited lower SACFOR estimates)). The Lough Swilly sub-population abuts the Islay Front; the southern sub-population abuts the Celtic Sea Front to the east, and the northeast sub-population is bounded to the north and south by the

	1950s/2000s	1950s/2010s	2000s/2010s
No change	2	1	1
Increases			
Colonizations	0	1	4 ^a
1-step	3	1	2
2-step	1	3	0
Decreases			
1-step	0	5	4
2-step	1	0	0
Extirpations	4 ^a	1	0

Note: Colonizations denote when *Sabellaria alveolata* is classed as present after being classed as Not Seen (absent) in the preceding comparable sampling period. 1-step and 2-step changes indicate either a one or two step SACFOR change (e.g. Common to Abundant = 1-step, Frequent to Abundant = 2-step). Extirpations denote when *S. alveolata* was classed as Not Seen after being classed as present in the preceding comparable sampling period.

^aDenotes three locations in the northeast where *S. alveolata* was present in 1950s, not seen in 2000s but then recolonized the same locations in the 2010s. See Figure 4 for graphical representation.

TABLE 1 The number of locations representing each category of abundance change between sampling periods where *S. alveolata* was present on at least one of the three sampling periods

Western Irish Sea Front and gyre (Figure 2). These alignments with the three tidal fronts were first identified in the 1950s and confirmed in the warmer 2000s and 2010s (Figure S2). Importantly, no reliable positive records were ever found between the Islay and Western Irish Sea Front (the locations of the two leading edges), which appears to be a persistent gap in the distribution despite warming temperatures and being characterized by apparently suitable habitat—a rocky coastline interspersed with beaches.

Of the 60 locations that were common to the three survey periods (1950s, 2000s, 2010s), *S. alveolata* was observed in all three sampling periods at seven locations (12%) and absent in all three sampling periods at 48 locations (80%). There was evidence of increases, decreases, extirpations and (re)colonizations among sampling periods (Figure 4, Table 1). Of the 11 locations where *S. alveolata* was present in the 1950s, it increased in abundance at four locations (36%) in the 2000s, all on the south and west coasts. It also decreased at five locations (45%); four of which were potential extirpations, and three of which were in the northeast. Of the three potential extirpations in the northeast, it recolonized three locations in the 2010s and was also found to colonize a new location on the south coast where it had not been found previously (Figure 4). This equates to a difference of 36% and 55% of locations exhibiting increases (between 1950s and either the 2000s or the 2010s) under the conservative and less conservative methods, respectively. Further to the 3-way time comparison, a number of locations had two or more records enabling comparison between the 1950s and either the 2000s or 2010s. Considering this additional information from four locations (all outside the northeast), one location exhibited a 1-step increase and three others exhibited new observations; potentially new colonizations, but not range extensions.

All but one of the potential temporary extirpations mentioned above were in the northeast. *Sabellaria alveolata* may have

experienced extirpations at a further six locations in this region over longer timescales (Figure 5). A museum specimen from 1872 for Kilkeel, Northern Ireland (~70 km south of Strangford Lough) implied the existence of *S. alveolata* reefs that formed sheets of up to 5 cm height (Figure 5 insert). A targeted search in 2018 discovered only a single live individual, and a single empty tube at two locations in the vicinity. Similarly, there were many reports of positive observations at Rossglass in the 1950s and 1960s including one reference to a “sabellarian belt approximately 1.8 m in depth extends for 185 m” (Williams, 1953). No *S. alveolata* was observed at Rossglass in 2014, and it was reported as present but dead in 2017. Some of the earliest references to *S. alveolata* in what is now the Republic of Ireland are from north of Dublin where presences were reported from Howth and Lambay Island, forming “great masses, covering the rocks and forming quite a conspicuous feature in the landscape” between Portmarnock and Malahide (Southern, 1910). It has since disappeared from all of these locations (Figure 5). Of the four locations in the northeast for which SACFOR abundances are given for 2013–2018, only Glasdrumman and Balbriggan supported populations classed as Common or Abundant (Figure 4b).

3.2 | Distribution modelling

Cross-validation of BRT predictions across independent spatial blocks yielded an area under the curve (AUC) of 0.88, suggesting a high degree of reliability in presence/absence classification. Moreover, BRT spatial predictions of *S. alveolata* distribution also qualitatively match regional patterns of observed occurrences (Figure 6a,b). Of the 12 environmental variables included in the model, wave height, tidal amplitude, stratification index, and

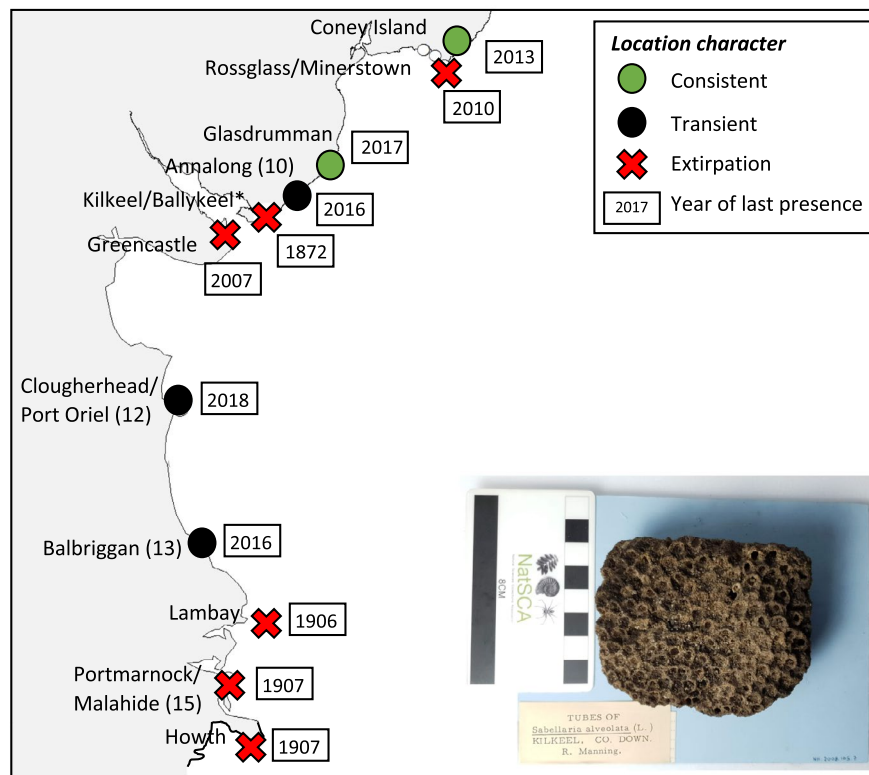


FIGURE 5 Spatio-temporal comparison of *Sabellaria alveolata* distribution and abundance in the northeast. Locations shown here were all sampled since 2005, have a minimum of two records separated by at least 30 years to represent a temporal comparison and indication of resilience across the region. Numbers in brackets indicate location number of the four locations that featured in the three-way time comparison in Figure 4. Historical records (i.e. 1872–1907) exist for a number of locations in this region (Kilkeel, Lambay, Malahide/Portmarnock, Howth), enabling some very long-term comparisons. Locations where *S. alveolata* was observed at least twice and at least once since 2013 are indicated by the black dot; locations where *S. alveolata* is perceived to have been extirpated are indicated by the red crosses; locations where *S. alveolata* has repeatedly been recorded as present and are considered important locations for *S. alveolata* are indicated by the green dots. Below lists the number of records and % presences (i.e. P or a SACFOR score) at each location. Years in which a SACFOR score was assigned are detailed in brackets. P = Present, A = Abundant, C = Common, F = Frequent, O = Occasional. Coney Island: 5 records, 1985–2013, present in 100% of records. Rossglass/Minerstown: 15 records, 1958–2014, present in 73% of records. Glasdrumman: 9 records 1985–2018, Present in 55% of records (C/A in 2016, 2017, 2018). Annalong: 17 records 1958–2016, present in 23% of records (R in 1985, 2016). *Kilkeel/Ballykeel: 4 records 1872–2018, present in 100% of records but museum specimen indicates that whilst reefs were present in 1872, only a single live worm and a single unoccupied tube were observed in 2018. Greencastle: 4 records 1985–2015, present in 50% of records but not observed since 2007. Port Oriel/Clougherhead: 12 records 1952–2018, present in 17% of records (O in 1958, 1984). Balbriggan 1958–2016: 4 records, present at 75% of records (O in 1958, C in 2013, F in 2016). Lambay: 2 records 1906–2005, present in 50% of records. Portmarnock/Malahide: 6 records 1907–2018, Present in 17% of records. Howth: 7 records 1907–2005, present in 14% of records. Photo credit: Paolo Viscardi, National Museum of Ireland—Natural History, Dublin

substrate type were the four most influential variables (in decreasing order) (Figure 6b). Probability of presence marginally increases with exposure to waves, up to a threshold of 1.8 m in significant wave height, beyond which *S. alveolata* occurrence is highly unlikely. *Sabellaria alveolata* predicted occurrence is low in areas where tidal amplitude is <1.8 m, and reaches an optimum where tidal amplitude is between 1.8–2.7 m. Its occurrence is also most likely in regions of higher stratification (stratification index > 3.2, Figure 6b). It typically occurs on rock and boulder, sand, muddy sand and mixed sediment but is typically absent from sandy mud or coarse sediment-dominated substrates (Figure 6b). Minimum sea surface temperature was the fifth most important environmental variable (with a ~ 7% contribution to model predictions). However, its influence is limited to probability of occurrence marginally

increasing when minimum temperatures are above ~ 6°C (See Appendix S2).

We also considered the interactions between the most influential variables (Figure S3). There was a significant interaction between mean wave height and tidal amplitude, stratification index, substrate type, minimum SST and wind speed respectively. In general, when wave height is >1.8 m (i.e. in exposed areas), probability of *S. alveolata* occurrence is marginal and other variables have little influence on model predictions. *Sabellaria alveolata* is predicted to thrive in areas where exposure to waves is moderate (wave height between 1.3–1.8 m), in particular where tidal amplitude is moderately high (between 2–2.5 m), in stratified waters (stratification index > 3.5), when minimum SST is above 6°C and when wind speed is between 11–12 m/s.

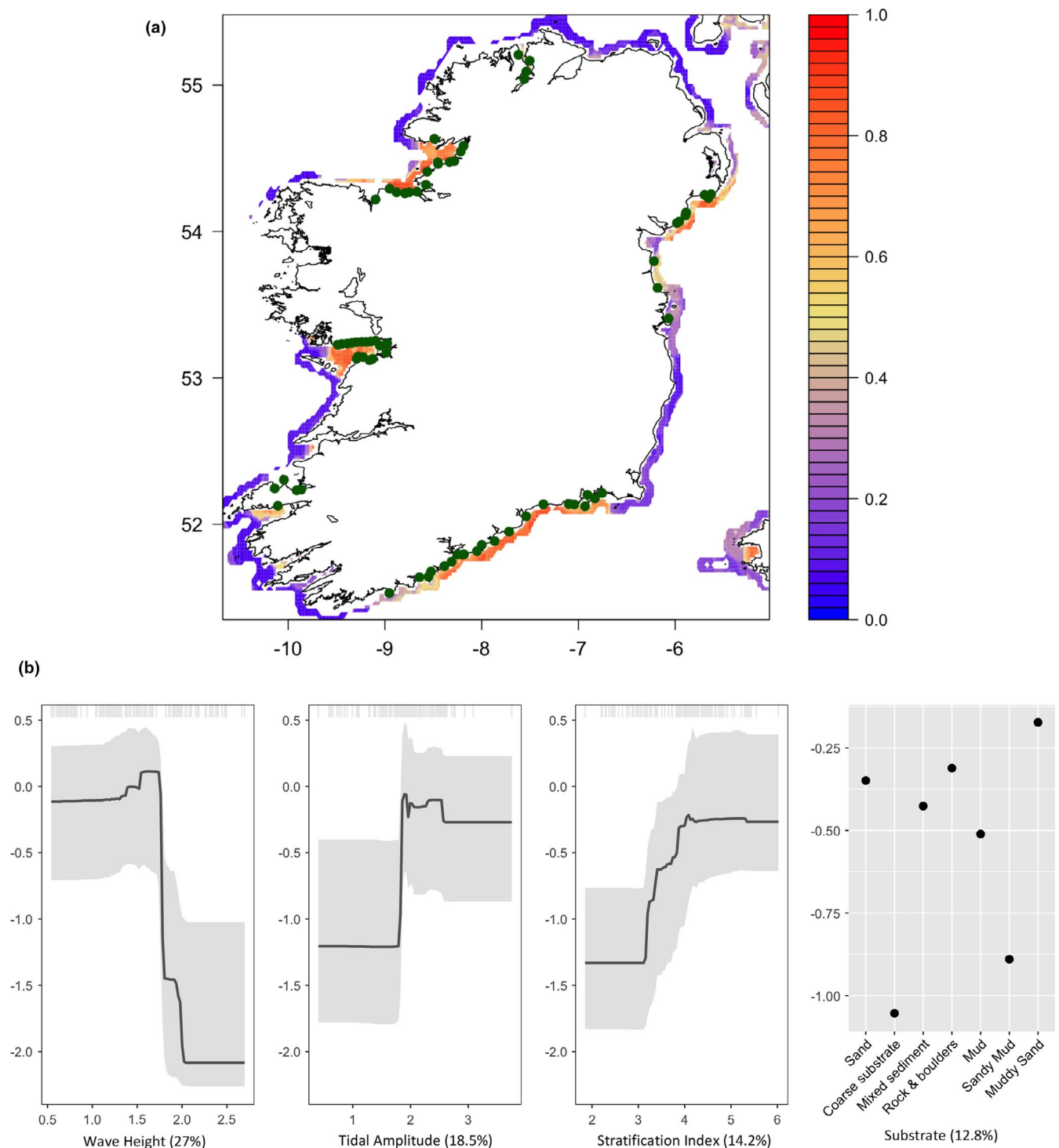


FIGURE 6 Spatial predictions from Boosted Regression Tree (BRT) models expressed as (a) probability of presence. Post-2013 surveys where *Sabellaria alveolata* was reported as 'present' are marked by green dots. (b) Partial influence of the four most influential variables: mean wave height (27%), tidal amplitude (18.5%), stratification index (14.2%), substrate (12.8%) to Boosted Regression Tree (BRT) model prediction

4 | DISCUSSION

We provide a comprehensive account of broad-scale (>7,400 km) and long-term (182 years) changes in the distribution and abundance of a widespread ecosystem engineer towards its poleward distributional edge around Ireland. We collated 981 records of presences (33%

of records) and not found—presumed absences (67%). Collating absences over consecutive surveys not only provides strong evidence of true regional absences, but also enables much greater power in statistical model predictions. *Sabellaria alveolata* exhibited a discontinuous distribution with multiple discretely bounded regions, three of which persistently aligned with tidal fronts. Two of these fronts

represent coincident leading edges; one in the northeast and one at Lough Swilly, with a persistent distribution gap in between. Whilst it was restricted to six geographic regions, the sub-populations within these regions and the previously recognized edges appeared to be relatively stable through time, with evidence of local increases within the regions but no evidence of range extensions beyond the previously identified poleward range edge in the northeast (Crisp, 1989). Similarly, Bush (2015) found the poleward range edge in Britain to be persistent between the 1980s and 2012.

Despite mounting evidence that *S. alveolata* responds positively to warming temperatures and negatively to cold winters (Crisp, 1964; Firth et al., 2015; Mieszkowska et al., 2005), its two leading edges in Ireland appear to be stable. As such, it is perhaps more appropriate to refer to these as poleward-most range edges, rather than leading edges which may imply some degree of movement. In the face of continued warming, if the trailing edges catch up with the poleward-most edges, this important ecosystem engineer may be susceptible to extirpation and even extinction, unless it can adapt or disperse through other means (e.g. intentional or unintentional human-assisted migration (Firth, Knights, et al., 2016; Woodin et al., 2014)). The northeast appeared to be highly 'dynamic', with evidence of declines, potential local extirpations and recolonizations. In this region, it is considered that a combination of reduced wave weights and tidal amplitude, coupled with being surrounded by cooler summer waters outside the Western Irish Sea Front in addition to being bounded by unsuitable substrate to the south make these populations potentially vulnerable to extinction risk as discussed below.

Our modelling suggests a combination of suitable wave height, tidal amplitude, local water stratification and substrate type are primary determinants of local occurrence of *S. alveolata*. Mean wave height had the strongest influence and interacted significantly with many other environmental variables (tidal amplitude, stratification index, minimum SST and wind speed). *Sabellaria alveolata* is most likely to occur in areas where exposure to waves is moderate (1.3–1.8 m), but at wave exposures >1.8 m *S. alveolata* is unlikely to occur and other variables have little influence on model predictions. To a lesser degree, *S. alveolata* occurrence is also favoured in conditions where tidal amplitude is moderately high (between 2–2.5 m) and where water is stratified in the summer (stratification index > 3.5). Whilst minimum sea surface temperature (SST) was the fifth most important variable, it only had a marginal influence on predicted probability (~7%) of *S. alveolata* occurrence. In this region, SST variability was relatively narrow (i.e. 10.5–12°C and 4–7°C for mean and minimum SST, respectively), and thus, there is relatively little variance in temperature to explain. This is further exacerbated by temperature data being averaged over multiple years (Bates et al., 2018). Future work should consider the influence of extreme and prolonged periods of low temperatures, particularly during the reproductive season, when gametes and larvae may be negatively affected by low water temperatures.

Through comparing 60 locations across three time periods (1950s, 2000s, 2010s), we found that population increases were observed at one time or another at all but three locations. We also

discovered that *S. alveolata* underwent declines in the 2000s at 42% of locations where it was recorded as present in the 1950s. Of these declines, 80% were extirpations, 75% of which were in the northeast. The fact that it was subsequently recorded at all of these locations in the 2010s suggests eventual recovery following the potential occurrence of a damaging extreme event or a sustained period of colder weather following the 1950s surveys (Éireann, 2019). *Sabellaria alveolata* and other taxa (Firth et al., 2015, see Mieszkowska et al., 2007 for work on *Phorcus*; Southward, 1991 for work on barnacles) were severely impacted by the extremely cold winter of 1962/63 in North Wales, with extirpations lasting 40 years and recovery likely inhibited by colder conditions from the 1960s to late 1980s. Sampling of known Irish *S. alveolata* populations immediately following the 1962/63 cold winter revealed that populations in the northeast were worst affected with reports of up to 40% mortality, whilst locations outside the northeast only suffered reductions in extent and height or were "apparently unaffected" (Crisp, 1964). It is possible that the cold winter of 1962/63 played a role in the both the temporary (Figure 4), and potentially permanent extirpations of *S. alveolata* from the locations in the northeast (Figure 5) and reductions elsewhere.

Few populations in the northeast were classed as Common or Abundant on the SACFOR scale, meaning that they were unlikely to be forming high-density reefs which would buffer individuals from thermal extremes and other environmental perturbations (Bertness & Leonard, 1997). Southward and Crisp (1954) identified that rocky shore communities in the northeast were susceptible to excessive winter cooling of sea surface temperature due to the easterly and south-easterly aspect of the shoreline. Furthermore, some of the locations in this region are considered vulnerable to physical damage from snail (winkle) harvesters through trampling and breaking off chunks of reef (Preston & Portig, 2001). The dynamic nature of the northern part of *S. alveolata*'s range is likely due to a combination of factors including cooler temperatures (exacerbated by the easterly aspect, Firth, White, et al., 2016), damage from trampling and harvesting and limited dispersal or immigration in the presence of multiple tidal fronts, rendering these populations highly vulnerable.

These populations are perhaps even more vulnerable because they are likely to be genetically isolated. Population genetic analysis, whilst based on a single population from Galway Bay, shows that *S. alveolata* from Ireland are genetically differentiated from other European and North African populations (Muir et al., 2020). Genetic structure at the regional scale around Ireland has not yet been evaluated for this species, but hydrodynamic modelling studies suggest that barriers to dispersal could exist, most likely due to tidal fronts (Robins et al., 2013), restricting connectivity among discrete populations. For instance, the Western Irish Sea Front and gyre can promote local larval retention, self-recruitment and genetic isolation of mussel populations within the Irish Sea (Gosling et al., 2008), and the Islay and Celtic Sea Fronts can further prevent larvae entering the Irish Sea (Lynch et al., 2004; Wilmes et al., 2019).

Genetic diversity of *S. alveolata* is greatest in its northern part of the distribution in the Irish Sea and English Channel due to the preservation of genetic diversity in refugia over Pleistocene glacial cycles

(Rigal, 2005), making this hotspot of genetic diversity vulnerable to population instability. For example, population collapse following the extremely cold winter of 1962/63 (Firth et al., 2015) is evoked as the likely cause of reduced genetic variation in populations in the eastern Irish Sea (Nunes et al., accepted). Despite stochasticity being evident in local and regional populations (i.e. within the discrete regions shown in Figures 3 and 4), our results suggest a complex population structure in *S. alveolata* and 'portfolio effect' (Schindler et al., 2015) at an island-scale, arising from an interplay between connectivity, gene flow with local adaptation, environmental perturbations and recruitment. Hotspots of genetic diversity are likely in a fragmented network of metapopulations with only occasional genetic interchange with different source populations. Such occasional recruitment may lead to Allee effects (decreased population growth or fitness at small population sizes), but any exchanges may buffer these and prevent local adaptation. Ongoing investigations into the dispersal and population genetics of *S. alveolata* around Ireland will cast further light on this.

Sabellaria alveolata reefs and their surrounding sedimentary habitats are known to support species of commercial importance (Dubois et al., 2002; Plicanti et al., 2016; Schimmenti et al., 2015) and the worms themselves are also collected as fishing bait, particularly in the Mediterranean (Gambi et al., 1992). In France, *S. alveolata* reefs have long been exploited for bivalves, causing the authorities to restrict harvesting activities in 1970 after a marked decline of the Mont-Saint Michel reef (Dubois et al., 2002). Recently, the non-native oyster, *Magallana* (formerly *Crassostrea*) *gigas* has become increasingly abundant on *S. alveolata* reefs in Mont-Saint Michel (Dubois et al., 2006), exacerbating physical damage to the reefs directly through overgrowth on worm tubes and indirectly through physical damage by harvesters (Dubois et al., 2002). Further information on damage caused by harvesting and associated invasive species would be beneficial for informing on how multiple stressors affect the vulnerability of this species.

The historical reach of this study coupled with the fine-scale mapping revealed persistent regional sub-population boundaries that align with tidal fronts, two of which are northernmost range edges. Crisp (1989) was the first to point out that intertidal fauna showed discontinuities around fronts in Ireland due to the impact of mixing through tidal energy. In that paper, he also suggested that long stretches of sandy coast that were subjected to severe scouring contribute to the biogeographic distribution patterns of both warm-adapted and cold-adapted species. The absence of *S. alveolata* in the southern Irish Sea between Dublin and Carnsore Point can largely be explained by the existence of long stretches of sandy coast. Here, we provide quantitative evidence that a combination of suitable substrata and a suite of hydrographic variables (tidal amplitude, stratification index and in particular, wave height) may act as environmental filters (Webb et al., 2002) and are likely to be key explanatory variables that underpin the distribution and persistence of *S. alveolata*. These can be used to predict the presence of this ecologically important and conservation priority species. Importantly, our habitat suitability modelling only considered the adult life history stage of

S. alveolata. Further work is needed to examine the relationship between environmental variables and larval dispersal limitation. For instance, it is possible that tidal fronts are acting as barriers to larval dispersal (e.g. Pringle et al., 2017), preventing *S. alveolata* advancing further eastwards along the northern Irish coastline or northwards through the Irish Sea. A greater understanding of why these hydrographic features act as barriers to the dispersal of some species and not others would help inform conservation and management plans for species that are vulnerable to climate change.

5 | CONCLUSIONS

In 1858, Edward Forbes drew his "general limit of southern types" (Figure 1, herein Forbes' Line) illustrating the distributional limits of marine species. Only through the relatively recent advancement of oceanographic research (1970s onwards) have links between the location of this line and major hydrographic features, including tidal fronts been made. Here, we quantitatively show that *S. alveolata* has a discontinuous distribution with two poleward-most range edges and six discretely bounded regional sub-populations. Using a combination of statistical model outputs and expert judgement, we identified a potential suite of specific mesoscale hydrographic niche requirements and thresholds required for population success. We also showed that the sub-population boundary edges that align with tidal fronts were largely stable over the past 62 years; this is despite (a) global and regional increases in sea surface temperatures that would predict range extension by this species, and (b) local and regional population fluctuations within the range that are associated with climate change and extreme weather events. This suggests that a combination of specific niche requirements associated with frontal regions have facilitated the long-term regional stability of this species, but may in the future act as barriers to range extension. Thus, these environmental boundaries may limit the capacity of this important ecosystem engineering species to redistribute in response to future climate change.

ACKNOWLEDGMENTS

Dedication: This paper is dedicated to Edward Forbes FRS FGS (1815-1854) for his pioneering work on biogeography. Alfred Russel Wallace is often referred to as the "Father of biogeography" and Wallace's Line between Borneo and Sulawesi is globally recognized. The line drawn by Forbes representing the "general limit of southern types" is less well known. Perhaps it was the coining of the term "Wallace's Line" and advocating of the concept by the influential Thomas Henry Huxley that facilitated this line becoming the most famous biogeographic demarcation in the world. Since then, a large number of major biogeographic boundary zones have been identified globally, but few have actually been named. We propose the naming of "Forbes' Line" (Figure 1) in recognition of Forbes' pioneering biogeographic work. The authors wish to thank the Irish Research Council and Campus France Ulysses Programme, the Irish Marine Institute and the Marine RDTI Measure Programme, the Linnean

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PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ddi.13224>.

DATA AVAILABILITY STATEMENT

All data used in this paper are available in: Curd, Cordier, et al. (2020). A broad-scale long-term dataset of *Sabellaria alveolata* distribution and abundance curated through the REEHAB (REEf HABitat) Project. SEANO. <https://doi.org/10.17882/72164>. All scripts are also available in the Appendix S2: https://aurelienboye.github.io/Firth-et-al-DDI/Supplementary_materials.html

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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